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Covariation between understorey light environments and soil resources in Bornean mixed dipterocarp rain forest

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Abstract: Variation in understorey irradiance is both a cause and consequence of the structure and dynamics of closed-canopy forests, which are also influenced by soil nutrients and water availability. We tested the hypothesis that understorey light regimes differ among four mixed dipterocarp forest types that share the same rainfall, but grow on different soils along an edaphic gradient at one site in Borneo. Based on data from photosynthetically active radiation sensors deployed at 1-m height at 36 locations for 351 sensor-days, we found significant soil-related variation in irradiance. The more productive forest types on clay and fine loam had lower daily photosynthetic photon flux density (PPFD) than those on the more nutrient-depleted and better-drained sandy loam and loam. They also had fewer moderate to high-intensity sunflecks, and a greater proportion of their daily PPFD came from low-intensity light. Understorey irradiance did not, however, monotonically decline with increasing soil resources. Forests on intermediate soils had greater irradiance than those with more and less soil resources, due to steeper slopes. Plant communities arrayed on resource gradients are commonly used to test hypotheses of environmental factors driving their assembly. Our results indicate that consideration of multiple resource dimensions in such tests is critical.

Key Words: environmental gradients, forest understorey, Malaysia, soil texture, sunflecks, tree regeneration, tropical forest

INTRODUCTION

Community-level patterns in plant species diversity, composition and functional-trait variation are often linked to differences in resource availability along environmental gradients (McGill *et al.* 2006), which are often defined with respect to the resources required for plant growth and survival (soil mineral nutrients, water and light). Gradients defined with respect to one resource may nonetheless also vary with respect to other resources. For example, forests growing on soils of different texture or along elevation gradients often have different disturbance regimes, creating covariation between these environmental factors and light (Matson & Boone 1984, Myster & Fernandez 1995, Ohkubo 2007a, 2007b; Richards 1996, Wells *et al.* 1998).

Feedbacks involving differential plant growth provide a mechanism by which resources can vary in disparate ways along gradients (Chapin *et al.* 1987, Pearson *et al.* 2003). Denser forest canopies have been observed to grow on more fertile, moister soils, casting greater shade in the understorey (Ashton 1964, Ashton & Hall 1992, Coomes & Grubb 1996). The degree of shading results from several interacting characteristics of the overstorey, including the biomass of leaves and their sizes, inclinations and longevities and the branching structure of tree crowns (Coomes & Grubb 2000). Variation in light environments between canopy gaps of different sizes and the forest understorey is well-documented (Chazdon & Fetcher 1984, Dalling *et al.* 1998, Denslow *et al.* 1998, Hartshorn 1980, Whitmore 1978), and there is also widespread evidence of finer-scale spatial variation in understorey light among microhabitats within closed-canopy forest (Canham *et al.* 1994, Coomes *et al.* 2005, Montgomery & Chazdon 2001, Poorter & Arets 2003, Whitmore & Wong 1959, Yoda 1974). What remains poorly understood is how understorey light regimes vary

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between neighbouring closed-canopy forest types that experience the same rainfall, but grow on different soil types.

Quantifying soil-related differences in understorey irradiance is important for understanding the growth and competitive interactions of juvenile trees because even small differences in photosynthetic photon flux density (PPFD) and the frequency and intensity of sunflecks, short bursts of direct photosynthetically active radiation (PAR), affect carbon gain (Chazdon 1986, Koizumi & Oshima 1993, Leakey *et al.* 2003, 2005; Zipperlen & Press 1997). Furthermore, light-defined niches of tree species can be finely partitioned (Barker *et al.* 1997), even among shade-tolerant tree species (Kobe 1999, Montgomery & Chazdon 2002, Poorter & Arets 2003). Recent studies have found a greater diversity of light-defined niches in forests on more-fertile, moist soil, compared with adjacent soil types that were more nutrient-limited and well-drained (Coomes *et al.* 2009).

We used an edaphic gradient underlying mixed dipterocarp forest in Malaysian Borneo to investigate covariation between the availabilities of understorey light and soil resources. This region is well-known for having a high turnover of tree species between soil-defined forest types (Ashton 1964, Baillie *et al.* 1987, Brunig 1974) due to specialization of species on different soils (Davies *et al.* 2005, Paoli *et al.* 2006, Potts *et al.* 2002). We tested the hypothesis that regimes of PAR differ significantly in the understorey of rain forest growing on four soil types along an edaphic gradient in Borneo. Soils along this gradient range from coarse loams that are sandstone-derived, nutrient-depleted and well-drained, to clays that are shale-derived, less nutrient-depleted and less well-drained (Baillie *et al.* 2006, Russo *et al.* 2010, Tan *et al.* 2009), but the forests share the same rainfall regime, as they are located at one site. Variation in light regimes between and within forest types was characterized in terms of total daily PPFD and the frequency, duration and intensity of sunflecks and in terms of their seasonal variation between the non-monsoon season and the generally cloudier, early monsoon season.

METHODS

Study site

This research was conducted in Lambir Hills National Park, Sarawak, Malaysia (4°11′N, 114°01′E). The Park encompasses 6800 ha of lowland mixed dipterocarp forest with the highest tree species richness recorded in the Palaeotropics (Ashton & Hall 1992, Lee *et al.* 2002). Rainfall is *c.* 3000 mm y^{-1}, with all months averaging > 100 mm (Watson 1985). Despite the lack of a well-defined dry season, there is seasonal variation in rainfall (Palmiotto 1998): the monsoon season, which brings greater monthly average rainfall, occurs approximately from November to February, with other times of year receiving less rainfall. In 1991, a 52-ha plot (hereafter, Lambir) was established in the Park following standardized methods (Condit 1998) and pegged with permanent markers at every 20-m grid corner (Figure 1). Floristic composition, stand structure, soils, soil nutrient and water contents, and geomorphology of Lambir are described elsewhere (Baillie *et al.* 2006, Lee *et al.* 2002, Russo *et al.* 2010, Tan *et al.* 2009).

The high species richness of this region is at least partly attributable to high beta-diversity, arising from substantial turnover of tree species composition between soil-defined habitats (Ashton 1964, Baillie *et al.* 1987, Potts *et al.* 2002). Soils range from coarse loams that are sandstone-derived, leached, nutrient-depleted and well-drained, with substantial raw humus, to clays that are shale-derived, less nutrient-depleted and less well-drained, with little raw humus. The distributions of most tree species in Lambir are strongly biased with respect to four soil habitats defined based on variation in nutrients (total C, N and P, and exchangeable K, Ca and Mg) and elevation at a 20 × 20-m scale (Davies *et al.* 2005). Ranked in ascending order of nutrient content and descending order of particle size, they are: sandy loam, loam, fine loam and clay (Table 1). In addition to variation in mineral nutrients, soil volumetric water content at 0–10 cm depth is significantly higher on the clay, relative to sandy loam, at all times of year (Russo *et al.* 2010). Furthermore, elevation and slope vary significantly among soil types: the sandy loam and clay soils occur at the highest and lowest elevations, respectively, and the loam and fine loam soils occur at intermediate elevations in Lambir (Baillie *et al.* 2006). The loam and fine loam soils are located on steep slopes, where there are more frequent landslips (Ohkubo 2007a, 2007b).

Measurement of understorey light and slope

Photosynthetic photon flux density (PPFD) was measured in the understorey of forest on each of the four soil types using photosynthetically active radiation (PAR) sensors (LI-190SA quantum sensor, LiCor Biosciences, Lincoln, Nebraska, USA) from 8 November–7 December 2007 and 28 May–21 June 2008. The first sampling period represents the early monsoon season, whereas the second sampling period (non-monsoon season) encompasses a period of relatively less rainfall. Sensors were arrayed in groups of three at randomly selected 20 × 20-m grid points (locations) on each soil type. Each sensor was placed 5 m from the grid point, in one of the four directions parallel to the plot axes. Sensors were mounted on tripods

Table 1. Mean total nitrogen (%), total phosphorus (mg kg^{-1}), pH, exchangeable magnesium ($cmol_c$ kg^{-1}) and calcium ($cmol_c$ kg^{-1}), and elevation (m) for the four soil types in the Lambir plot (Davies *et al.* 2005). Significant differences among soil types are indicated by different lowercase letters, with standard errors following the means.

Soil type	N	Total N	Total P	pH	Mg	Ca	Elevation
Sandy loam	766	0.093 ± 0.001^{a}	43.7 ± 0.7^{d}	4.64 ± 0.01^{a}	0.12 ± 0.01^{d}	0.21 ± 0.01^{c}	193.8 ± 0.7^{a}
Loam	184	$0.099 \pm 0.003^{a,c}$	66.5 ± 2.3^{c}	4.41 ± 0.01^{b}	0.15 ± 0.01^{c}	0.22 ± 0.01^{c}	183.1 ± 1.4^{b}
Fine loam	270	0.107 ± 0.002^{b}	103.3 ± 2.2^{b}	4.32 ± 0.01^{c}	0.19 ± 0.01^{b}	0.30 ± 0.00^{b}	152.6 ± 1.4^{c}
Clay	80	$0.107 \pm 0.003^{b,c}$	133.6 ± 4.1^{a}	4.43 ± 0.04^{b}	0.70 ± 0.04^{a}	0.52 ± 0.01^{a}	138.8 ± 1.7^{d}

and levelled at a height of 1 m. Sensors were kept at each location for 72 h then moved to a new location. In 2007, seven locations each were sampled on the loam and fine loam soils, and 14 locations each were sampled on the sandy loam and clay soils, for a total of 189 sensor-days; in 2008, six and 12 locations, respectively, were sampled, for a total of 162 sensor-days. This placement of sensors was designed to sample spatial variation in light within soil types at both coarse scales (variation among locations) and fine scales (variation among sensors within a location).

PPFD from each sensor was recorded using battery-powered data-loggers (CR-800 and CR-1000; Campbell Scientific, Logan, Utah, USA). In 2007, data were scanned every 5 s, with average, maximum and total PPFD recorded every 15 min and 24 h. In 2008, data were scanned and recorded every second, with average, maximum and total PPFD recorded every 15 min and 24 h. Two PAR sensors were mounted in a tower < 1 km from the plot, over the forest canopy and completely exposed to the sky, measuring the maximum possible PPFD given cloud-cover. Data from the canopy and understorey sensors were recorded at the same frequency.

The slope in degrees was calculated using standard methods (Condit 1998) for each location, based on elevation data from the Lambir plot. Four slopes were calculated from the four corners of each 20×20-m quadrat surrounding each location, and the average was used.

Statistical analysis

Total daily PPFD was calculated in the understorey and over the canopy for each sensor-day based on the 15-min totalized data from 06h00–18h00 in 2007 and 2008. Relative total daily PPFD (hereafter, relative PPFD) in the understorey was calculated as a percentage of the above-canopy PPFD (the average of data from the two sensors) on that day ((understorey PPFD/over-canopy PPFD) $\times$ 100). Relative PPFD was analysed using a linear, mixed-effects model with normally distributed errors using the Mixed Procedure in SAS software version 9.2 (SAS Institute Inc., Cary, NC, USA). Slope, soil type and their interaction were treated as fixed effects, and location, sampling date (date) and sensor number (sensor) were treated as nested random effects: location (habitat), date (location) and sensor (location), where the parentheses indicate the grouping variable within which effects were nested. For purposes of variance partitioning, all effects were treated as fixed effects in order to calculate coefficients of determination for each. Relative PPFD was logarithmically transformed prior to analysis to improve normality of residuals. Over-canopy PPFD was used to test for seasonal differences in light availability using a general linear model with normally distributed errors and season (early monsoon or non-monsoon) as a fixed effect.

The frequency of sunflecks in 2007 and 2008 was modelled as a binomial process, $m_j \sim \text{Binomial}(N_j, p_j)$, where N_j is the total number of 15-min sampling intervals in a day from 06h00–18h00, m_j is the number of those 15-min intervals in which the maximum PPFD exceeded 20, 50 or 100 μmol m^{-2} s^{-1}, and p_j is the expected probability of a sunfleck occurring in an interval. Thus, a 15-min interval was categorized as having experienced a sunfleck of low, medium or high intensity based on whether the maximum PPFD exceeded 20, 50 or 100 μmol m^{-2} s^{-1} in that interval. These thresholds of light intensity were selected based on previous definitions of sunflecks (Chazdon & Fetcher 1984, Koizumi & Oshima 1993). Variation in the expected probability of a sunfleck occurring was analysed using generalized linear mixed-effect models employing a logit link function (McCullach & Nelder 1989) using the Glimmix Procedure in SAS software version 9.2 (SAS Institute Inc., Cary, NC, USA). Slope, soil type and their interaction were treated as fixed effects, and location, date and sensor were treated as nested random effects, as in the analyses of relative PPFD. Data from 2007 and 2008 were analysed separately for both relative PPFD and sunfleck probability, because one set of locations that was sampled in 2007 was not sampled in 2008. To identify seasonal differences, statistical tests were also performed for the identical subset of locations that were sampled in both seasons. The probability distribution of the maximum PPFD within a 15-min interval, across all sampling sensors, locations and days within a soil type and season were tested for differences (1) between forests on different soil types in the same season and (2) between seasons in forests on the same soil type. The latter comparisons used the identical set of locations for both seasons. These differences were identified using a series of two-sample Komolgorov–Smirnov tests, which test whether two empirical distributions come from the same probability distribution.

To assess patterns in dynamic radiation at finer temporal scales, PPFD was also scanned and recorded at 1-s intervals in 2008. The number of seconds (duration) during which PPFD fell within eight intensity bins was counted at each sensor location from 06h00–18h00 over 18 d. The independence of sunfleck duration and intensity across soil types was tested using log-linear models on the binned data (Agresti 1990). For each sensor location, the per cent of total PPFD contributed by sunflecks of different intensities was also calculated. Differences due to soil type and slope were tested using multivariate analysis of variance (MANOVA). Data were square-root transformed to improve normality. Model selection using Akaike's Information Criterion (AIC) (Burnham & Anderson 2002) was used to select the best-supported model for all analyses.

Table 2. Correlations between slope and total daily photosynthetic photon flux density in the understorey of four forest types in Borneo underlain by sandy loam, loam, fine loam and clay in the early monsoon and non-monsoon seasons.

Forest type	r	P
Early monsoon season – all locations		
Sandy loam	−0.06	0.539
Loam	0.31	0.016
Fine loam	−0.02	0.888
Clay	0.04	0.661
Early monsoon season – locations sampled in both seasons		
Sandy loam	0.02	0.830
Loam	0.30	0.038
Fine loam	−0.23	0.090
Clay	0.07	0.457
Non-monsoon season		
Sandy loam	−0.19	0.044
Loam	0.38	0.005
Fine loam	−0.18	0.191
Clay	0.20	0.041

RESULTS

Seasonal variation in total daily photosynthetic photon flux density

Above the forest canopy, total daily PPFD was significantly higher in the non-monsoon than the monsoon season ($F_{(1,65)} = 5.31$, P = 0.024). Total daily PPFD averaged (± SE) 35.6 ± 0.16 mol m^{-2} in the non-monsoon season and 31.2 ± 0.15 mol m^{-2} in the early monsoon season.

Soil-related variation in total daily photosynthetic photon flux density

The slope of the locations at which PPFD was sampled differed significantly among soil types ($F_{(3,38)} = 9.53$, P < 0.001). Loam was steeper than all other soil types (all P < 0.005), but no other comparisons differed significantly. For both seasons, slope correlated strongly with total daily PPFD only in the understorey of forest on loam soil (Table 2). However, the model with only the main effect of forest type had the lowest AIC for all data sets, and so the effect of slope and its interaction with forest type were removed (ΔAIC relative to the full model: early monsoon season, all locations, 25.3; early monsoon season, subset of locations sampled in both years, 24.1; non-monsoon season, 17.5). Variation between the forests on the four different soil types in total daily PPFD at 1-m height explained 13% and 11% of the total variation in PPFD in the early monsoon and non-monsoon season, respectively. The PPFD varied significantly among these forests in both the early monsoon season (Figure 2a; all locations: $F_{(3,38)} = 3.63$, P = 0.021; subset of locations sampled in both seasons: $F_{(3,32)} = 3.29$, P = 0.033) and non-monsoon seasons (Figure 2b; $F_{(3,32)} = 3.10$, P = 0.040). Overall, the dominant pattern in both seasons was that forest on the clay soil had the darkest understorey and that forest on loam and fine loam had the brightest understorey, but which comparisons showed statistically significant differences were not always consistent. In the early monsoon season, the forest understorey on clay was significantly darker than on both loam and fine loam (based on all locations sampled) and than on loam only (based on locations sampled in both seasons). In the non-monsoon season, the forest understorey on clay was significantly darker than on both sandy loam and loam. In the early monsoon season, the forest understorey on loam also had significantly greater PPFD than did the sandy loam, based on locations sampled in both seasons. The disparate results between datasets based on all locations sampled were largely due to one location on fine loam near a large gap from a landslip that was sampled in the early monsoon, but not the non-monsoon, season.

Within forest types, course- and fine-scale spatial effects accounted for more of the total variation in PPFD than did temporal effects. Variation between locations within a forest type (coarse scale) and between sensors at a location (fine scale) accounted for 45% and 37% in the early monsoon season (all locations) and for 41% and 41% in the non-monsoon season, respectively, of the total variation in PPFD. In contrast, variation in PPFD among days at a location accounted for only 3% and 4% of the total variation in PPFD in the early monsoon (all locations) and non-monsoon seasons, respectively.

Table 3. Significant differences within the understorey of Bornean rain forest growing on four soil types in the frequency of sunflecks of low, medium and high intensity (> 20, > 50 and > 100 μmol m^{-2} s^{-1}, respectively) in two seasons. Sunflecks were defined based on the maximum photosynthetic photon flux density observed in 15-min intervals. Test statistics are shown for the main effect of forest type, with numerator and denominator degrees of freedom (ndf and ddf, respectively). Statistically significant post hoc comparisons between forest types, tested after finding a statistically significant main effect of forest type, were assessed at P < 0.05. Abbreviations for forest types: SL = forest on sandy loam; L = forest on loam; FL = forest on fine loam; C = forest on clay.

Sunfleck intensity	F-value (ndf, ddf)	P	Significant post hoc comparisons
Early monsoon season - all locations			
Low	3.50 (3, 37.3)	0.025	C < SL, C < L, C < FL
Medium	3.22 (3, 36.6)	0.034	C < SL, C < L, C < FL
High	2.42 (3, 35.6)	0.082	–
Early monsoon season - locations sampled in both seasons			
Low	2.33 (3, 31.3)	0.093	–
Medium	2.12 (3, 31.3)	0.118	–
High	1.99 (3, 30.5)	0.136	–
Non-monsoon season			
Low	3.39 (3, 29.9)	0.031	C < SL, C < L, FL < SL
Medium	2.97 (3, 28.9)	0.049	C < SL
High	2.56 (3, 28.7)	0.074	–

Soil-related variation in frequency and intensity of sunflecks

Forests types differed strongly in the frequency of understorey sunflecks of different intensities in the early monsoon (Figure 3a) and non-monsoon (Figure 3b) seasons, based on data recorded every 15 min. In all within-season pairwise comparisons of forests on different soils, the probability distributions of maximum PPFD for each soil type were significantly different from each other (all P < 0.001). Forests on the same soil type also differed in their probability distributions of maximum PPFD across seasons (all P < 0. 001).

The model with only the main effect of forest type had the lowest AIC for all data sets, and so the effect of slope and its interaction with forest type were removed from models. The frequency of sunflecks with low and medium, but not high, intensities varied significantly among forest types in both the early monsoon and non-monsoon seasons, but differences among forest types in sunfleck frequency and intensity shifted between seasons (Table 3). In the early monsoon season, based on all sampled locations, the forest on clay had the lowest frequency of low- and medium-intensity sunflecks, whereas the forest on sandy loam was intermediate in frequency of low- and medium-intensity sunflecks. The forest on loam had the highest frequency of low-intensity sunflecks, and the forest on fine loam had the highest frequency of medium-intensity sunflecks. Based only on locations sampled in both

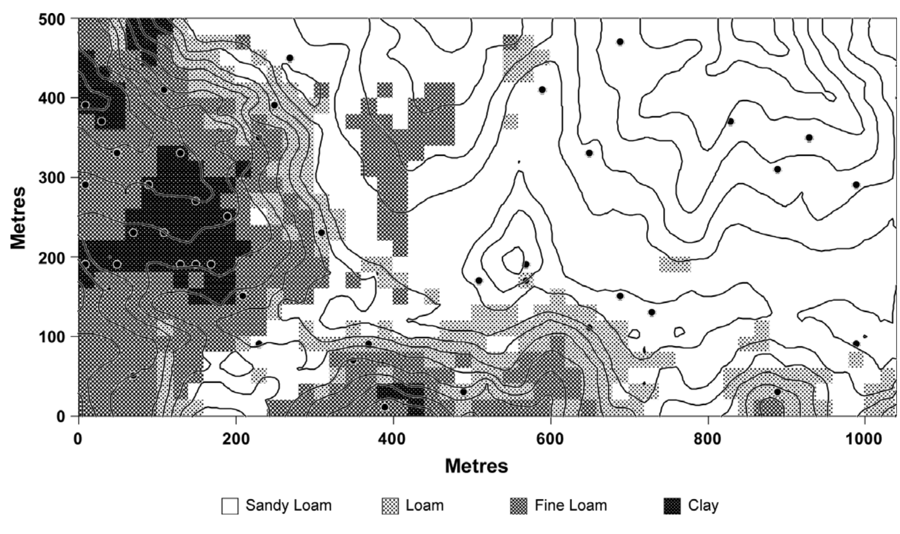

Figure 1. Map of the 52- ha forest dynamics plot at Lambir Hills National Park, Malaysian Borneo, showing soil types, elevation contours (14 m) and sampling locations (filled circles).

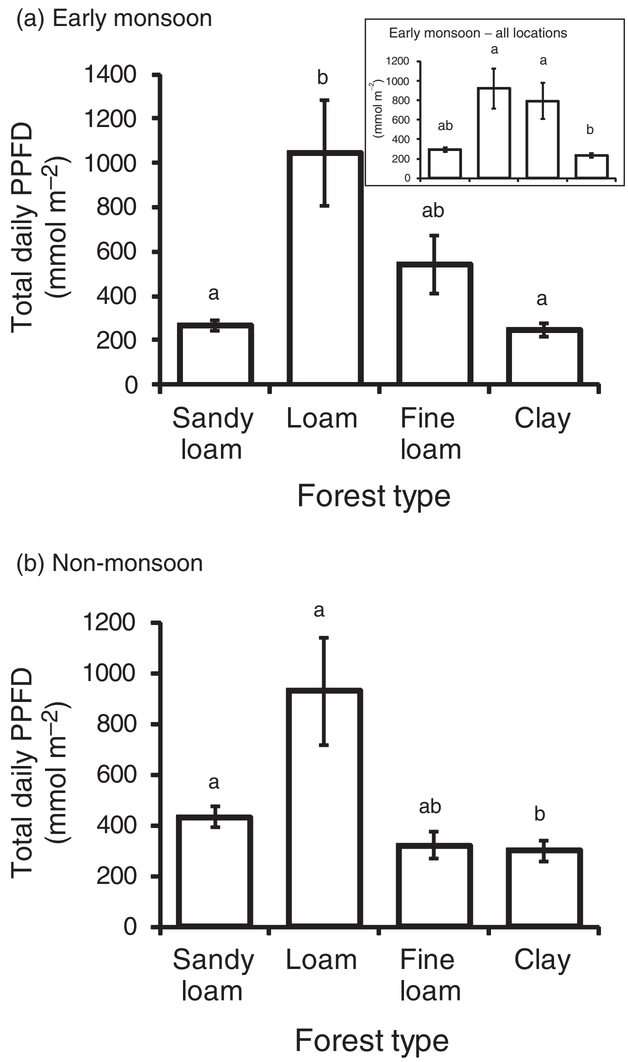

Figure 2. Average total daily photosynthetic photon flux density (PPFD) in the understorey of Bornean rain forest underlain by four soil types. The inset shows comparisons between forest types in the early monsoon season (November 2007) based on all sampled locations (189 sensor-days at 7 (loam and fine loam) and 14 (sandy loam and clay) locations per forest type), and the main chart shows comparisons based on the subset of those locations that were also sampled in the monsoon season (a). The main chart shows comparisons between forest types in the non-monsoon season (May 2008; 162 sensor-days at 6 (loam and fine loam) and 12 (sandy loam and clay) locations per forest type) (b). Error bars are ± 1 SE. Different letters over bars indicate significant differences between soil types, based on relative PPFD.

seasons, however, there were no significant differences among the forests in the early monsoon season. In the non-monsoon season, the forest on clay again had the lowest frequency of low- and medium-intensity sunflecks, but, in contrast to the wetter season, the forest on sandy loam had the highest frequency of low- and medium-intensity sunflecks. The forests on loam and fine loam were intermediate in the frequency of low- and medium-intensity sunflecks.

Based on PPFD recorded every second during the monsoon season, the duration and intensity of sunflecks differed significantly across forest types. The log-linear model with all effects and interactions had the lowest AIC (448), and a likelihood ratio test strongly favoured inclusion of the three-way interaction ($P < 0.001$), indicating that sunfleck intensities and durations were not independent across soil types. Both long-duration and high-intensity sunflecks were rare on all soil types. The understorey of forest on sandy loam and loam had higher frequencies of moderate to high-intensity sunflecks, compared with the fine loam and clay soils, where PPFD was more concentrated into short-duration sunflecks of low-intensity. These patterns in sunfleck intensity were confirmed in analyses of the per cent of total PPFD received in 3 d at locations on each soil type (Figure 4). The effect of forest type on the multivariate variance in PPFD was significant (Pillai's $P = 0.420$, $df = 3$, $P = 0.006$). Univariate tests within each sunfleck PPFD category revealed that more of the total PPFD in the understorey of fine loam and clay was contributed by the lowest intensity sunflecks, compared with sandy loam and loam. In contrast, the per cent of the total PPFD contributed by moderate- to high-intensity sunflecks was higher in the sandy loam and loam understorey, compared with fine loam and clay. However, forest types differed in the relationship between slope and the per cent of total PPFD contributed by sunflecks of differing intensities, and this effect was strongest for the forest type on loam, which had the steepest slopes (forest type–slope interaction: Pillai's $P = 0.411$, $df = 3$, $P = 0.008$; Figure 5). Univariate tests within each sunfleck category demonstrated that for the understorey on sandy loam, clay, and fine loam, slope had no effect on the per cent of total PPFD contributed by sunflecks of any intensity, except that on fine loam, steeper locations had a lower per cent contributed by high intensity sunflecks (100–500 μmol m^{-2} s^{-1}; Figure 5d). In contrast, on loam, locations with steeper slopes had a greater per cent of total PPFD contributed by high-intensity sunflecks (25–50 and 50–100 μmol m^{-2} s^{-1}; Figure 5b and 5c), but had a lower per cent contributed by the lowest intensity sunflecks (0–5 μmol m^{-2} s^{-1}; Figure 5a).

DISCUSSION

The light regimes that juvenile trees experience in the understorey of closed-canopy forest have a profound influence on above-ground competitive interactions, life histories and allometries of trees as they vie for a position in the canopy (Pickett & White 1987), with consequences for the maintenance of species diversity (Ricklefs 1977). Variation in light regimes is, however, both a cause and consequence of above-ground vegetation, the structure

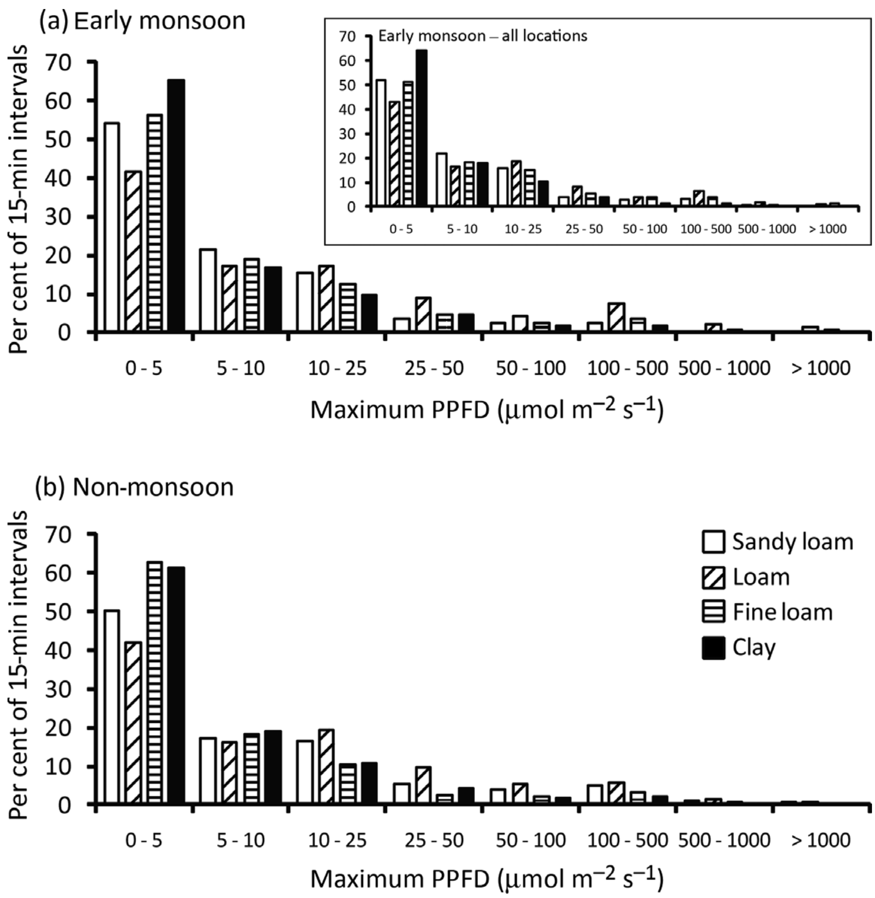

Figure 3. Distribution of the intensity of sunflecks in the understorey of Bornean rain forest underlain by four soil types. The per cent of daytime 15-min intervals in which the maximum photosynthetic photon flux density (PPFD) fell into each light intensity class is shown for the understories of sandy loam, clay, loam and fine loam soils, across all sampling dates, locations and sensors within soil type and season. The inset shows comparisons between forest types in the early monsoon season (November 2007) based on all sampled locations (189 sensor-days at 7 (loam and fine loam) and 14 (sandy loam and clay) locations per forest type), and the main chart shows comparisons based on the subset of those locations that were also sampled in the monsoon season (a). The main chart shows comparisons between forest types in the non-monsoon season (May 2008; 162 sensor-days at 6 (loam and fine loam) and 12 (sandy loam and clay) locations per forest type) (b).

of which is influenced by other resources, such as soil nutrients and water availability, and disturbance. We found evidence of such feedbacks involving above- and below-ground resources: there was significant variation in both total daily PPFD and sunfleck frequency and intensity in the understorey of forest growing on four soil types along an edaphic gradient in Borneo. Although the number of sample locations on each forest type was limited, the results we obtained using PAR sensors were consistent with a study of two of these forest types using 98 hemispherical photographs, which found saplings in the understorey on sandy loam to experience 6% greater canopy openness compared with those on clay soil (Russo *et al.* 2010). Rank differences in understorey light regimes between soil types were consistent between seasons, although above-canopy PAR was lower in the monsoon, relative to the non-monsoon, season. In addition to this soil-related variation, we also found understorey light regimes to vary strongly at finer spatial scales within a forest type and to vary with the slope of the land surface for two forest types.

Causes and consequences of soil-related variation in light regimes

In our study, forests on the different soil types varied in several edaphic factors, including soil texture, soil nutrient and water availability, elevation, slope, and aspect. The independent effects of all of these factors cannot be distinguished here, but we nevertheless found significant soil-related effects on understorey insolation among these forest types. Our results are consistent with studies from tropical and temperate forests that also found understorey light availability to decrease with increasing availability of soil resources (Coomes & Grubb 2000).We did not, however, find a simple pattern of monotonic decline, as forests on the intermediate soil types had

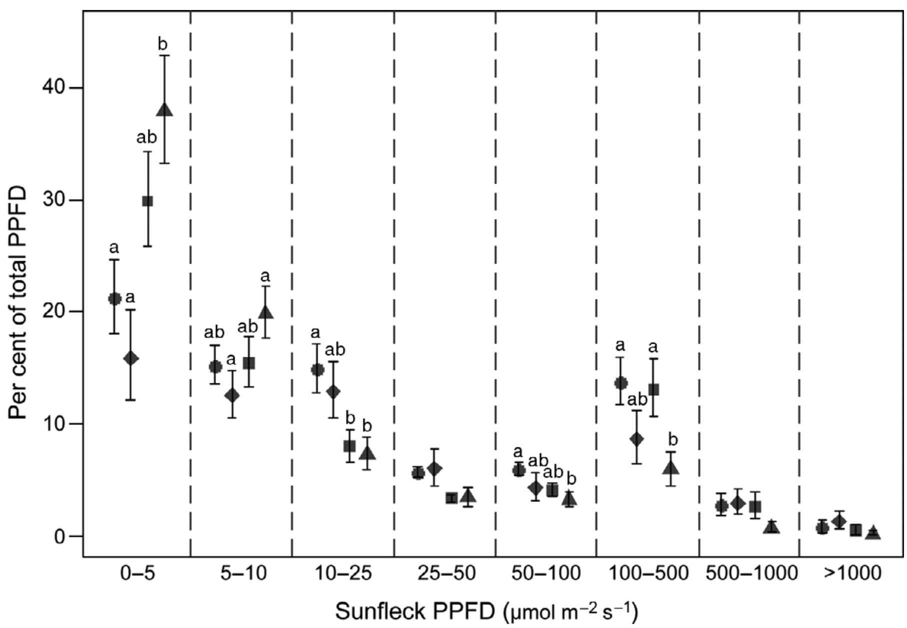

Figure 4. The per cent of total photosynthetic photon flux density (PPFD) over 3 d contributed by sunflecks of different PPFD in the understorey of Bornean rain forest underlain by four soil types in the non-monsoon season (May 2008). Points are means across sample locations, with standard error bars, grouped by sunfleck PPFD category. Different letters within each category indicate significant differences among soil types within that category, based on univariate tests after a significant overall multivariate analysis of variance. For categories lacking letters, there were no significant differences among soil types. Symbols: circle, sandy loam; diamond, loam; square, fine loam; triangle, clay.

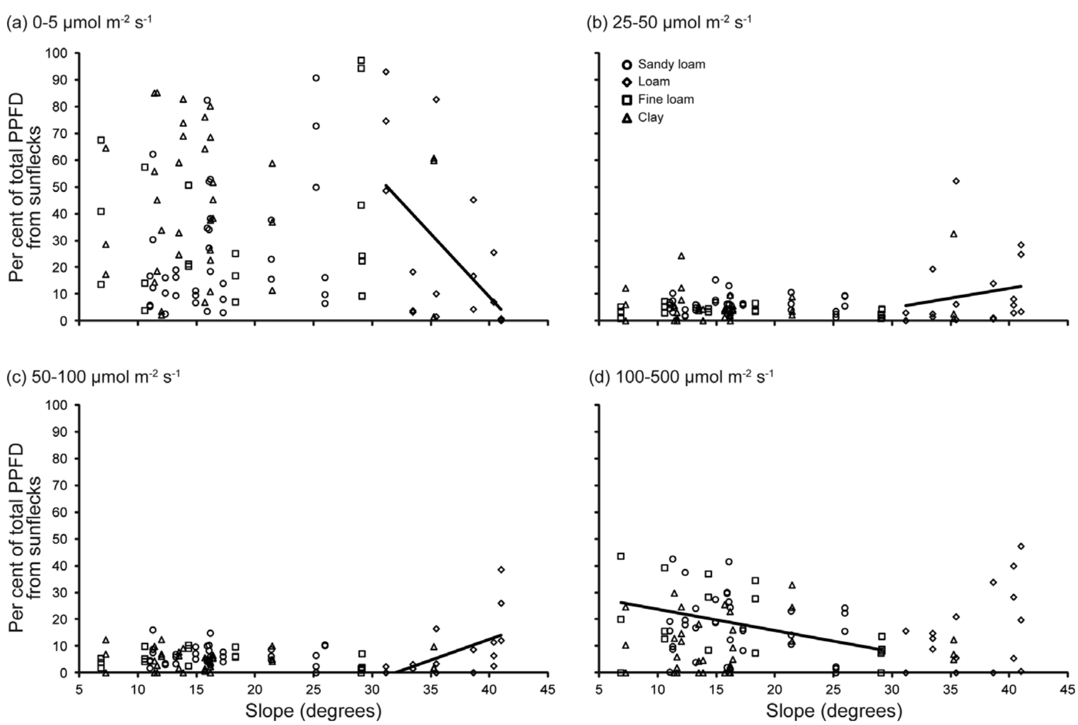

Figure 5. Variation between slope and the per cent of total photosynthetic photon flux density (PPFD) over 3 d contributed by sunflecks of different PPFD in the understorey of Bornean rain forest underlain by four soil types in the non-monsoon season (May 2008). Only sunfleck PPFD categories with a significant interaction between forest type and slope are shown: 0–5 umol m^{-2} s^{-1} (a), 25–50 umol m^{-2} s^{-1} (b), 50–100 umol m^{-2} s^{-1} (c), and 100–500 umol m^{-2} s^{-1} (d). Points represent sample locations, with the least-squares regression lines for forest types having a non-zero slope of the relationship between per cent of total PPFD and slope.

greater light availability than those at either end of the gradient. This was always true for the forest on the loam soil, but only true for the fine loam soil in the early monsoon season, largely due to one location on fine loam near a large gap from a landslip that was sampled in the early monsoon, but not the non-monsoon, season.

The within and between forest-type variation in light regimes at Lambir may have several origins. First, the four forest types examined here occur within a 52-ha area, and so do not result from variation in rainfall. Nevertheless, due to differences in soil texture, elevation and slope, the same rainfall produces significant variation in water availability in each forest type (Russo *et al.* 2010). Despite constant rainfall, our results comparing irradiance in forests on sandy loam and clay are still consistent with studies along rainfall gradients, which generally have found leaf area index to decrease in parallel with water availability, accompanied by an increase in light penetration (Coomes & Grubb 2000). Second, the variation in light transmission among the forests along this edaphic gradient is likely to be related to the divergent leaf and crown traits of the tree species comprising the different assemblages associated with each soil type. Average leaf size of canopy trees is larger on the clay and fine loam than on the sandy loam or loam soil types at Lambir (Ashton 1964, Ashton & Hall 1992), which would reduce PAR transmission to the understorey. Variation among the different forest types at Lambir in the sizes of canopy leaves, which are better lit, is most likely a consequence of differences in soil resource supply, since leaves with larger specific leaf area are generally found on soils with greater nutrient and water availability (Wright *et al.* 2002; S. E. Russo, unpubl. data). Furthermore, the decreased penetration of light on clay occurs in opposition to the generally shorter leaf life spans of the clay specialists (S. E. Russo, unpubl. data), in parallel with forests on soil gradients in the temperate zone (Coomes & Grubb 2000). Third, the four forest types vary not only in below-ground resources, but also in slope. The loam soil and parts of the fine loam soil comprise steep slopes with greater occurrence and larger sizes of landslips than do the clay, low-lying parts of fine loam, and sandy loam soils (Ohkubo 2007a, 2007b; Yamakura *et al.* 1996). Steep slopes would result in larger, more frequent canopy openings and could explain why the decline in understorey irradiance was not monotonic with increases in soil resource availability. In addition, forest types differed in the relative impact of slope versus other edaphic factors, such as resource availability, on understorey insolation. Because they differed the least in slope, comparisons between forests on clay, fine loam and sandy loam are likely to better reflect the effect of soil texture differences than of slope on understorey irradiance. In contrast, the steep slopes of loam likely explain why the understorey on this forest type had the highest insolation, since only in this forest type did slope correlate strongly with total daily PPFD and sunfleck frequencies and intensities.

Although we found significant soil-related differences in understorey irradiance among forest types, there was also substantial spatial variation within forest types. Tree species composition shifts dramatically among forests on these soil types (Davies *et al.* 2005), but the spatial distribution of species, even for soil specialists within forest types, also varies considerably. Spatial turnover in species composition within forest types likely contributes to finer-scale spatial variation in light transmission due to interspecific differences in leaf and crown traits (Canham *et al.* 1994, Turner *et al.* 2000). Furthermore, although most tree species distributions are strongly associated with categorically defined soil habitats (Davies *et al.* 2005), the within-soil variability in understorey irradiance suggests that finer-scale continuous variation in soil resources may also influence the species composition and leaf and crown traits that ultimately determine light transmission.

The different light regimes among the forest types along this edaphic gradient may have several consequences for forest structure and dynamics. It is well-established that even small differences in photosynthetic photon flux density (PPFD) and the frequency and intensity of sunflecks affect the growth of seedlings and saplings in the understorey (Chazdon 1986, Koizumi & Oshima 1993, Leakey *et al.* 2003, 2005; Zipperlen & Press 1997). We found that statistically similar total daily PPFD among these Bornean forest types nonetheless resulted from different distributions of sunfleck frequency and intensity, as did Chazdon (1986). Assuming that trees have the physiological capacity to respond to dynamic irradiance, we would expect these differences to translate into different photosynthetic responses, consequences for carbon gain, and growth rates (Chazdon & Pearcy 1991, Leakey *et al.* 2005). At Lambir, maximum rates of carbon assimilation are faster on average for tree species that specialize on the sandy loam soil type, compared with clay, which is contrary to expectations based only on soil resource availability (Russo *et al.* 2010). However, the reduced soil resources on sandy loam soil may ultimately limit carbon gain or shift carbon allocation below-ground or to making longer-lived tissues, since juvenile trees on this soil have the slowest diameter growth rates (Russo *et al.* 2005). The fastest diameter growth rates are achieved by trees on the loam and fine loam soils, followed by those on clay (Russo *et al.* 2005), paralleling the differences in PPFD and dynamic irradiance for these three soil types. These patterns suggest that competitive dynamics among juvenile trees may be dominated more by soil resource availability at the resource-poor end of this edaphic gradient and by understorey irradiance at the other end, as would be predicted by Tilman (1988). Faster predicted tree height growth, based on empirically parameterized allometric growth models, of tree species specializing on the clay soil, relative to sandy loam specialists, is consistent with this hypothesis (Heineman *et al.* 2011).

Differences among forest types in the frequency of sunflecks of varying intensities may also lead to soil-related differences in the range of light-regeneration niches available, resulting in diversification of tree crown and height allometries and allometric growth rates (Coomes *et al.* 2009, Heineman *et al.* 2011, Poorter & Arets 2003). Ultimately, these shifts in photosynthetic carbon gain and allometric growth responses are expected to sort tree species among soil habitats, resulting in differences in composition among forest types. Consistent with this idea, the frequency of light-demanding, fast-growing tree species is greater on the loam and fine loam soil types (Russo *et al.* 2005), which would further reinforce soil-related patterns of variation in light regimes due to increased light transmission through the canopies of early-successional species (Canham *et al.* 1994, Coomes & Grubb 2000).

Conclusions

Beyond the importance of understanding the causes and consequences of the plant–soil feedbacks generating soil-related variation in understorey light regimes, our study has implications for the methods used to infer factors important in the assembly of and competitive interactions in forest communities. First, our results bring renewed attention to the need to consider multiple resource dimensions when testing hypotheses about environmental factors driving plant community structure and dynamics along gradients (Chapin *et al.* 1987, Pearson *et al.* 2003). The availability of different resources along gradients can vary in opposing directions, generating opposing environmental selection pressures and hampering inferences concerning the relative importance of different abiotic factors in the assembly and functional trait variation of plant communities.

Second, basal area is often used as a metric of neighbourhood competition in forests, with greater basal area implying a shadier environment (Canham *et al.* 2006). At Lambir the forest on sandy loam has greater basal area and stem density compared with the forest on clay (Davies *et al.* 2005, Lee *et al.* 2002), yet understorey light availability varies in the opposite direction. These findings suggest that the relationship between standing basal area and light transmission to the understorey is not the same between these two forest types. It is therefore important to account for variation due to soil types when using standing basal area as a measure of competition for light between forest types in which floristic composition (Davies *et al.* 2005), leaf functional traits (S. E. Russo, unpubl. data) and canopy leaf structure (Ashton 1964, Ashton & Hall 1992) differ as greatly as they do between the forests on the different soil types at Lambir.

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